Title: **Thermal behavior alleviates thermal discomfort during steady-state exercise without affecting whole-body heat loss**

Authors: Nicole T. Vargas[1], Christopher L. Chapman[1], Blair D. Johnson[1], Rob Gathercole[2], Matthew N. Cramer[3], and Zachary J. Schlader[1,4]

Affiliations:

[1]Center for Research and Education in Special Environments, Department of Exercise and Nutrition Sciences, University at Buffalo, Buffalo, NY, USA

[2]lululemon athletica inc., Vancouver, BC, Canada

[3]Institute for Exercise and Environmental Medicine, Texas Health Presbyterian Hospital Dallas and University of Texas Southwestern Medical Center, Dallas, TX, USA

[4]Department of Kinesiology, School of Public Health, Indiana University, Bloomington, IN, USA

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Corresponding author:

Zachary J. Schlader, PhD

1025 E. 7th St.

Department of Kinesiology

Indiana University

Bloomington, IN 47405

Email: zschlade@indiana.edu

Abstract:

We tested the hypothesis that thermal behavior resulting in reductions in mean skin temperature alleviates thermal discomfort and mitigates the rise in core temperature during light intensity exercise. In a 27 ± 0°C, 48 ± 6% relative humidity environment, 12 healthy subjects (6 females) completed 60 min of recumbent cycling. In both trials, subjects wore a water perfused suit top continually perfusing 34 ± 0ºC water. In the behavior trial, the upper body was maintained thermally comfortable by pressing a button to perfuse cool water (2.2 ± 0.5ºC) through the top for 2 min per button press. Metabolic heat production (Control: 404 ± 52 W; Behavior: 397 ± 65 W, P=0.44) was similar between trials. Mean skin temperature was reduced in the behavior trial (by -2.1 ± 1.8ºC, P<0.01) due to voluntary reductions in water perfused top temperature (P<0.01). Whole body (P=0.02) and local sweat rates were lower in the behavior trial (P≤0.05). Absolute core temperature was similar (P≥0.30), however the change in core temperature was greater in the behavior trial after 40 min of exercise (P≤0.03). Partitional calorimetry did not reveal any differences in cumulative heat storage (Control: 554 ± 229; Behavior: 544 ± 283 kJ, P=0.90). Thermal behavior alleviated whole body thermal discomfort during exercise (by -1.17 ± 0.40 a.u., P<0.01). Despite lower evaporative cooling in the Behavior trial, similar heat loss was achieved by voluntarily employing convective cooling. Therefore, thermal behavior resulting in large reductions in skin temperature is effective at alleviating thermal discomfort during exercise without affecting whole body heat loss.

New and Noteworthy: This study aimed to determine the effectiveness of thermal behavior on maintaining thermal comfort during exercise by allowing subjects to voluntarily cool their torso and upper limbs with 2ºC water throughout a light intensity exercise protocol. We show that voluntary cooling of the upper body alleviates thermal discomfort while maintaining heat balance through convective rather than evaporative means of heat loss.

Keywords: Thermoregulatory behavior, exercise, heat balance, skin cooling

Introduction

Subjective perceptions of thermal discomfort give rise to thermal behavior (10). Thermal behavior is often deemed a physiological variable given that it directly complements autonomic thermoregulatory responses (e.g., sweating, skin blood flow, shivering) to regulate body temperature (48). Thus, thermal behavior is defined as a voluntary action that aims to establish a thermal environment (or microclimate) that promotes heat balance (47). For instance, when there is freedom to behaviorally thermoregulate during resting conditions, responses are elicited primarily by changes in skin temperature to alleviate thermal discomfort and prevent changes in core temperature (i.e., maintain heat balance) (40). The efficacy of thermal behavior to promote heat balance, and consequently, maintain thermal comfort during exercise is less clear.

During exercise, the initial rate of metabolic heat production is not immediately offset by active cutaneous vasodilation (23) or sweating, despite that initial increases in sweat rate happen almost immediately (54). Consequently, core temperature rises in the early stages of exercise. However, in a compensable thermal environment, the rise in core temperature levels off after 30-40 min of exercise, a point at which autonomic thermoeffectors facilitate sufficient heat loss to achieve and maintain heat balance (19). Our laboratory has identified that both autonomic and behavioral thermoeffectors are simultaneously activated during exercise (57). In such instances, thermal behavior is recruited in proportion to the magnitude of increases in core and mean skin temperatures, and skin wettedness, the latter of which occurs secondary to sweat buildup on the skin (56).

Our studies, and those of other laboratories that have examined thermal behavior during exercise, have used models in which the behavioral responses were isolated to a finite skin surface area, such as the hand (8) or posterior neck (56), which have little effect on temperature or whole-body thermal discomfort (33). Whole-body immersion in water has also been used to study thermal behavior (4). However, this model negates any contribution of skin wettedness. In addition to these methods, thermal behavior during exercise has been examined using self-selected exercise work rate, whereby voluntary increases (in the cold) or decreases (in the heat) in the rate of metabolic heat production are used to quantify thermal behavior (30, 41, 44, 45). Importantly, in these studies, subjects were required to continue exercising (i.e., maintain metabolic heat production above resting levels) throughout the study despite continued levels of thermal discomfort. Thus, the studies conducted to date do not allow for insights regarding the effectiveness of thermal behavior to alleviate thermal discomfort and promote heat balance during exercise. Therefore, the purpose of this study was to test the hypothesis that engaging in thermal behavior that elicits voluntary reductions in mean skin temperature during exercise alleviates thermal discomfort and attenuates elevations in core temperature.

Methods

This study was approved by the Institutional Review Board at the University at Buffalo, and performed in accordance with the standards set by the latest revision of the declaration of Helsinki, except for registration in a database. Each subject was fully informed of the experimental procedures and possible risks before giving informed written consent prior to participating.

Subjects

Twelve young healthy adults (6 females, age: 24 ± 3 y, height: 171 ± 10 cm, weight: 73 ± 14 kg, BSA: 1.8 ± 0.2 m^2, body fat: 16.4 ± 6.6%) participated in this study. Subjects were free from any known cardiovascular, metabolic, neurologic or psychological diseases. All subjects were physically active, normotensive, non-smokers, not taking medications and were in the normal range for cognitive ability. Female subjects were not pregnant, which was confirmed via a negative urine pregnancy test, and self-reported to be normally menstruating. All trials for females were performed during the first 10 days (i.e., follicular phase) following self-identified menstruation or during the placebo phase of their oral contraceptives (n=4), a period in which estrogen and progesterone are at their lowest levels. Although there appears to be little influence of the menstrual cycle on exercise-induced changes in core temperature, particularly in trained individuals (22, 25, 28), controlling for the menstrual cycle may be important considering increased thermal sensitivity has been suggested to occur during the luteal phase (22). Subjects visited the laboratory on three occasions. Visit one was a screening and familiarization visit and visits two and three were experimental trials.

Instrumentation and measurements

Height and weight were measured with a stadiometer and scale (Sartorius Corp. Bohemia, NY, USA), and body surface area was calculated accordingly (5). Skinfold thickness was measured in triplicate at the chest, axilla, triceps, sub scapula, abdomen, suprailiac, and thigh (Harpenden, Baty International, UK). Body density was calculated from the sum of skinfold measurements for males (20) and females (21) and used to estimate percent body fat (50). Cognitive ability was measured using the Montreal Cognitive Assessment to ensure subjects were in the normal range for cognitive ability (35). This is important because of the perceptual nature of this study. Urine specific gravity was measured in duplicate using a refractometer (Atago USA, Inc., Bellevue, WA, USA).

Beat to beat blood pressure was continually measured via the Penaz method (Finometer Pro; FMS, Amsterdam, The Netherlands), which was confirmed via manual auscultation of the brachial artery. Heart rate was measured via a wireless transmitter (Polar, Kempele, Finland). Skin blood flow was measured continually on the dorsal surface of the left forearm under the water perfused top via integrated laser Doppler flowmetry (Periflux System 5010, Perimed, Stockholm, Sweden). Cutaneous vascular conductance was calculated as skin blood flow perfusion units divided by the mean arterial pressure.

Metabolic data were obtained via a mouthpiece with a one-way non-rebreathing valve at the end of 10 and 20 min pre-exercise time points, at 15 and 30 minutes during exercise. Minute ventilation was calculated from expired airflow measured via a heated pneumotachometer (Hans Rudolph, Inc. Shawnee, KS, USA, n=7) or flow turbine (Vacumetrics, Inc., Ventura, CA, USA, n=5), which was continuously integrated over 1 min and corrected to standard temperature, pressure, dry (STPD). Whether expired airflow was measured using the pneumotachometer or flow turbine was kept constant within a subject. The fractions of expired oxygen and carbon dioxide (VacuMed, Ventura, CA, USA) were continuously measured from a 3 L mixing chamber. Oxygen uptake and carbon dioxide production were calculated using the Haldane Transformation. The rate of metabolic heat production was calculated from oxygen uptake and the respiratory exchange ratio (see Appendix A).

Core temperature was measured using a wireless telemetry pill (HQ Inc., Palmetto, FL, USA) that was ingested approximately 60 min prior to any experimental testing. One subject had contraindications to swallowing the core temperature pill. In this subject, rectal temperature was measured using a rectal thermistor (Mon-a-therm; Mallinckrodt Medical, Inc., St Louis, MO, USA) inserted 10 cm beyond the anal sphincter. Mean skin temperature was measured as the unweighted average of ten thermocouples attached to the left side of the body on the lower shin, posterior calf, posterior thigh, anterior thigh, abdomen, chest, supra-scapula, forearm, shoulder and on the middle of the forehead (52). This unweighted average was chosen based on the recommendation that ten sites are most appropriate for studies examining thermal comfort (29).

Local sweat rate was measured by tightly securing a capsule that covered 3.9 cm^2 of the skin 3-5 cm below the axilla, on the mid-axillary line (under the water perfused top, n=12), and on the anterior thigh (outside of any clothing, n=6). The capsule was tightly taped to the skin after applying it with double sided adhesive. Dry nitrogen was perfused through the capsule at a rate of 0.5 L/min, allowing for measurement of the water vapor from the skin exiting the gas capsules to be continuously measured by capacitance hygrometry (HMT130, Vaisala, Woburn, WA, USA). Local sweat rate was calculated by multiplying the humidity output by the flow rate of the dry nitrogen and dividing that value by the surface area of the capsule. Whole body sweat loss was estimated from the change in nude body weight pre- to post-trial, and is reported in grams.

Relative humidity of the skin was measured via 8 hydrochron iButtons (Maxim Integrated Products Inc., San Jose, CA, USA) placed directly adjacent to a thermocouple at the forehead, chest, shoulder, forearm, supra-scapula, abdomen, anterior thigh and calf. At each location, the iButton was raised 6 mm off the skin using a custom-made capsule that allowed airflow to pass through. The distance of 6 mm was chosen because it ensured that the humidity sensor of the iButton would not become artificially supersaturated due to a droplet of sweat entering the hygrosensor (55, 56). Relative humidity from the iButtons and skin temperature from the adjacent thermocouple placed on each site were used to determine the water vapor pressure of the skin using standard calculations as previously reported (13). Local skin wettedness was calculated according to the methods of Gagge (17). The equations for calculating local water vapor pressure and local skin wettedness can be found in Appendix B. Whole body mean skin wettedness was calculated as the equally weighted average of all 8 local skin wettedness sites (55).

Thermal behavior was measured using a technique modified by those of Cabanac et al. (8, 10) and currently employed by our laboratory (42, 55, 57, 58). The exception is that instead of the voluntary modification of a relatively small surface area of skin, thermal behavior in the present study involved voluntarily controlling the temperature of the torso and arms. Pilot testing indicated that this surface area was sufficient to affect whole-body thermal comfort during exercise. Specifically, the employed technique required subjects to control the temperature of their upper body by voluntarily perfusing cold water through a tube-lined top (Med-Eng, Ottawa, ON, Canada) covering their arms and torso. The water-perfused suit top was continually perfused with thermoneutral water (34.0 ± 0.1ºC). However, subjects were freely permitted to press a button when they desired cold water (2.2 ± 0.5ºC) to perfuse the water perfused suit top. The temperature of the water baths were recorded in 5 min intervals. Pressing of the button initiated the turning of valves to allow cold water to run through the suit for 2 min. Following cooling, a mandatory 1 min wash out period was required, in which thermoneutral water again perfused through the suit top. Subjects were instructed to keep their upper body thermally comfortable throughout the experiment and were instructed to behave as often as necessary. A compression top was placed over the water perfused top to ensure contact with the subject's upper body. The reduction in upper body skin temperatures with cold water perfusion of the suit was perceived within ~25 s. The unweighted average of upper body skin temperature (i.e., shoulder, forearm, chest, supra-scapula and abdomen) and the temperature of the effluent fluid exiting the water perfused suit top provided objective and continuous measures of thermal behavior (8, 10).

Perceptual measures for the whole-body and upper body (i.e., torso and limbs) were taken every 10 min to the nearest 0.5 units using the following standard visual analogue scales: thermal sensation (1=cold, 4=neutral, 7=hot (16)); thermal comfort (1=comfortable, 4=very uncomfortable (16)); and skin wettedness (+3=very wet, +2=wet, +1=slightly wet, 0=neutral, -1=slightly dry, -2=dry, -3=very dry (13)) and sweating perception (0= none, 10 = most ever (43)).

Partitional calorimetry was used to estimate dry and evaporative heat loss both under and outside of the water perfused suit top. Using these data, the rate of heat storage and cumulative heat gain throughout the protocol were estimated. Notably, this analysis was added post hoc based on the reported findings to help inform decision making regarding conclusions. Details of the partitional calorimetry methods can be found in Appendix C.

Study design and experimental protocols

At least 24 h prior to experimental testing, subjects reported to the laboratory and were familiarized with the water perfused top and the perceptual questionnaires. For the experimental trials, subjects arrived to the laboratory euhydrated, confirmed via urine specific gravity ≤1.020 (actual urine specific gravity – Control: 1.004 ± 0.006; Behavior: 1.005 ± 0.007), and having refrained from strenuous exercise, alcohol and caffeine for 12 h, and food for 2 h. During both trials, thermoneutral water perfused the suit top throughout, while during the behavior trial, subjects were free to behaviorally thermoregulate (receive 2ºC water through the water perfused top) for 2 min at a time. The control and behavior trials were separated by a minimum of 48 h. This was deemed acceptable because to our knowledge there is no evidence that exercise 48 h prior modifies the thermoregulatory responses to exercise. The control trial was always performed first so that subjects had a reference regarding the warmth and thermal discomfort generated by the light intensity exercise in the conditions employed herein. All experimental testing was conducted during the summer months in Buffalo, NY (outside temperature on experimental days – Control: 19 ± 4°C; Behavior: 20 ± 4ºC). Male subjects were shirtless under the water perfused top and females wore only a standard sports bra (energy bra, lululemon inc.). Both male and females wore running shorts (men or women's cut, lululemon inc.), and their own socks and athletic shoes.

The experimental trials took place in a moderate thermal environment (Control: 27 ± 0°C, 48 ± 11% relative humidity, Behavior: 27 ± 0ºC, 49 ± 11% relative humidity). Upon arrival at the laboratory, subjects ingested the wireless telemetry sensor and recorded their nude weight in a private room. Following ingestion of the pill and nude weight, subjects were not allowed to eat or drink anything until after the protocol was complete and a final nude body weight obtained. Subjects were then instrumented and sat on a mesh chair behind a standard upright cycle ergometer (Monark 828E, Sweden) for a 20 min baseline measurement period. Subjects remained in the recumbent position and began cycling on the ergometer for 60 min at a light intensity. Subjects watched non-stimulating documentaries (i.e., Planet Earth) throughout the entire protocol.

Data and Statistical Analyses

Data were continuously recorded at 125 Hz via a data acquisition system and binned as 60 s averages every 10 min (Biopac MP160, Goleta, CA, USA). Core temperature data are reported as absolute values, and are also presented as the absolute change from baseline. Whole body sweat losses were analyzed using paired t-tests. All other data were analyzed using a two-way repeated measures ANOVA for differences over time and between conditions. When the ANOVA revealed a significant F test, *a priori* Sidak post hoc comparisons were made between trials and over time (compared to the 20 min pre-exercise time point). All analyses were carried out using Prism (Version 7, GraphPad Software Inc., La Jolla, CA). For all analyses, *a priori* statistical significance was set at $P \leq 0.05$ and actual P-values are reported where possible.

Results

Exercise stimulus

The average absolute external workload was not different between control (70 ± 1 W) and behavior trials (70 ± 1 W, P=0.88). Mean arterial pressure did not differ between trials (P=0.64). However, mean arterial pressure increased at 10 min into exercise (P<0.01) and remained elevated in the control trial (P<0.01), but returned similar to baseline levels in the behavior trial thereafter (P≥0.70). Metabolic heat production (n=11, due to equipment issues with 1 subject) was not different between control (30 min: 401 ± 63 W; 60 min: 396 ± 69 W) and behavior (30 min: 401 ± 48 W; 60 min: 407 ± 57 W) trials (P≥0.44). The evaporative heat loss required to maintain heat balance (n=11, due to equipment issues with 1 subject) was reduced during exercise at 30 min in the behavior compared to control trial (Control: 296 ± 62, Behavior: 259 ± 96 W, P=0.01), but not at 60 min (Control: 291 ± 63; Behavior: 270 ± 71 W, P=0.21).

Body temperatures and mean skin wettedness

Mean skin temperature decreased in the behavior trial from 20 min into exercise compared to the control trial and remained lower throughout (P<0.01) (Figure 1A). Absolute core temperature at baseline and throughout exercise did not differ between the behavior (37.0 ± 0.3ºC) and the control (37.1 ± 0.2ºC, P=0.34) trials, but increased in both trials (P<0.01). The change in core temperature was greater in the behavior compared to control from 40 to 60 min of exercise (P≤0.03) (Figure 1C). Mean skin wettedness was not different between the behavior and control trials ($P=0.40$) (Table 1), but increased from baseline at 20 min into exercise and remained elevated throughout exercise for both control and behavior trials ($P<0.01$). That said, the absolute partial pressure of water at the skin was attenuated in the behavior trial compared to the control trial from 20 min into exercise and remained lower throughout ($P<0.01$) (Table 1).

Thermoeffectors

The temperature of the water perfused suit top and mean upper body skin temperature (indices of thermal behavior) were reduced in the behavior compared to control trial within the first 10 min of exercise and remained lower throughout ($P<0.01$) (Figure 2A&D). Forearm skin blood flow and cutaneous vascular conductance (Figure 2B&E) were not different between trials ($P\geq0.32$), but increased in both the control and behavior trials within the first 10 min of exercise, and remained elevated throughout ($P<0.01$). Local sweat rate under the water perfused top was lower in the behavior trial compared to the control trial at 20 min into exercise, and remained lower throughout ($P\leq0.01$) (Figure 2C). Similarly, local sweat rate outside of the water perfused suit was also attenuated in the behavior trial compared to control, but these differences were only significant at 30 min ($P=0.03$) and 60 min ($P<0.01$) time points (Figures 2F). Accordingly, whole body sweat losses were attenuated in the behavior trial (0.45 ± 0.10 kg) compared to the control trial (0.63 ± 0.20 kg, $P=0.02$).

Thermal perceptions

Subjects perceived their upper body to feel warmer and reported more thermal discomfort at 10 min into and throughout exercise ($P<0.01$) in the control trial compared to the behavior trial (Figures 3A&C). Thermal behavior also attenuated the rise in whole body sensations of warmth and thermal discomfort in th behavior compared to the control trial from 10 min of exercise and onwards ($P\leq0.04$) (Figures 3B&D).

Upper- and whole-body sweat perceptions were elevated during the control trial compared to behavior trial from 20 min into exercise and onwards ($P \leq 0.03$) (Table 1). Similarly, subjects perceived greater skin wettedness in their upper body during the control trial compared to the behavior trial from 10 min of exercise and onwards ($P \leq 0.03$) (Table 1). However, there were no differences in perceptions of whole body skin wettedness at any time point during exercise between control and behavior trials ($P \geq 0.10$) (Table 1).

Partitional calorimetry

Calculations of evaporative ($P \geq 0.52$) and dry ($P \geq 0.99$) heat losses outside of the suit top were not different between behavior and control trials, but increased during exercise in both trials ($P<0.01$) (Figures 4A&D). Evaporative heat losses under the suit top were not different between trials during baseline ($P \geq 0.08$), but increased during exercise compared to baseline in both trials ($P<0.01$). However, evaporative heat losses under the suit top were attenuated during exercise in the behavior trial compared to the control trial ($P<0.01$) (Figure 4B). In contrast, dry heat loss under the suit top was augmented in the behavior compared to control trial during exercise ($P<0.01$), while there was no increase in dry heat loss in the control trial during exercise ($P \geq 0.99$). Total evaporative heat loss was attenuated in the behavior trial compared to control ($P<0.01$) during exercise, however, total dry heat loss was greater in the behavior trial compared to the control trial during exercise ($P<0.01$) (Figures 4C&F). Accordingly, the estimated rate of body heat storage increased during exercise ($P<0.01$), but was not different between conditions ($P \geq 0.83$) (Figure 5A). Likewise, calculated cumulative heat storage during exercise was not different between the behavior (544 ± 283 kJ) and control (554 ± 225 kJ, $P=0.90$) trial (Figure 5B).

Discussion

The present study tested the hypothesis that voluntary reductions in skin temperature would alleviate thermal discomfort and mitigate the rise in core temperature during exercise. The present data partially support our hypothesis, such that thermal behavior alleviates thermal discomfort during exercise (Figure 3C&D). In contrast to our hypothesis, however, these data also indicate that thermal behavior during exercise does not affect the absolute core temperature response compared to when thermal behavior is not employed (Figure 1B). This finding was corroborated by our post hoc partitional calorimetry data that indicated that cumulative heat storage did not differ between the behavior and control trials (Figures 4&5). These data indicate that thermal comfort was maintained when thermal behavior was employed during light intensity aerobic exercise, despite not affecting whole-body heat loss.

When thermal behavior is studied at a local level (i.e., using a cooling stimulus at the hand (5, 7) or the neck (42, 56-58)), utilization of thermal behavior attenuates the rise in local thermal discomfort, with no measurable effect on the thermal status of the body (i.e., changes in core or mean skin temperature). Moreover, cooling the skin over a larger surface area during self-paced exercise alleviates whole body thermal discomfort and increases total work output (44). Thus, we hypothesized that thermal behavior, which was expected to reduce skin temperature on a relatively large body surface area, would promote thermal comfort by improving heat loss and attenuating the rise in core temperature. In support of our hypothesis, subjects voluntarily cooled their upper body skin temperature by up to 2.1 ± 1.8ºC (Figure 2B). Consequently, engaging in thermal behavior maintained upper body thermal comfort and alleviated whole body thermal discomfort throughout light intensity exercise (Figure 3C&D). Considering the effective cooling area was ~36% of body surface area, this finding was not surprising. To our knowledge, however, this is the first study to show that voluntary cooling effectively alleviates whole body thermal discomfort during exercise.

By definition, behavioral thermoregulation results in a preferred state of heat exchange that promotes heat balance (15, 47). Previous studies examining thermal behavior during exercise using self-paced protocols support this position. For example, voluntary reductions in exercise work rate in the heat attenuate the rise in core temperature, which occur secondary to reductions in metabolic heat production (26, 44, 53). In addition, we (46) and others (12) have identified that mandatory ~~and~~ constant upper body cooling during exercise in the heat attenuates the rise in core temperature. Thus, a secondary hypothesis was that thermal behavior resulting in large reductions in skin temperature would attenuate the rise in core temperature by augmenting heat loss from the skin to the water perfused suit top. In contrast to our hypothesis, the rise in core temperature was +0.2 ± 0.2ºC higher during the final 20 min of the exercise protocol when thermal behavior was allowed compared to when behavior was restricted (Figure 1C). This finding was particularly surprising in light of the importance of core temperature as a driver of thermal behavior (and thermal discomfort) during fixed intensity exercise (9). Nevertheless, this result may be supported by the observation of attenuated sweat rates both under and outside of the water perfused suit top during the behavior trial (Figure 2C&F). Previous findings support this observation, such that cooling prior to exercise (i.e., via ice slurry ingestion) has been shown to attenuate evaporative heat loss, resulting in greater heat storage (31). Moreover, experimental reductions in skin temperature during exercise reduce sweat rate (34). Thus, it is plausible that heat storage was greater when thermal behavior was employed and sweat rate was attenuated in the current study. However, we also observed that the absolute core temperature responses did not differ between the behavior and control trials (Figure 1B). Therefore, it is possible that differences in the absolute change in core temperature between trials were simply due to slight differences in baseline core temperature (i.e., baseline core temperature in the behavior trial was 0.1 ± 0.2ºC higher than in the control trial) that were within the error of the measurement (6). To further investigate this discrepancy in core temperature, we performed a post hoc partitional calorimetric analysis to investigate whether our core temperature responses were indicative of greater heat storage when given the option to behaviorally thermoregulate during exercise. These estimates revealed an attenuated evaporative heat loss underneath the water perfused top in the behavior trial, in support of our local and whole-body sweating responses (Figure

4B). In contrast, dry heat losses were greatly augmented by the cool water perfusing the top (Figure 4E). Thus, based on these heat exchange estimates, it appears that cooling of the skin likely resulted in attenuated evaporative requirements for heat balance, thereby lowering the rate of sweat output and actual evaporation in proportion to the amount of added dry heat loss (Figure 4C&F). As a result, there were no differences in the rate of body heat storage over time (Figure 5A) or cumulative heat storage (Figure 5B) between the trials. Therefore, we interpret these data to indicate that engaging in thermal behavior that reduces skin temperature to a large surface area in the environmental and exercise conditions employed herein, is unlikely to affect the core temperature response to exercise.

The reason for the seemingly divergent observations regarding the change in core temperature data versus the absolute core temperature and partitional calorimetry data are not inherently clear. We speculate, however, that they may be a consequence of using the wireless telemetry pill, which is moving throughout the gastrointestinal tract over time and may be more readily influenced by reflex mediated redistributions in visceral blood volume. Thus, it is possible that higher skin temperatures in the control trial resulted in comparatively more blood shunted away from the gastrointestinal tract in an effort to promote heat loss. In contrast, in the behavior trial, while the upper body was being actively cooled, more warm blood may have been maintained in the visceral tissues, which would explain a greater rise in core temperature despite no differences in cumulative heat storage. Notably, our measures of skin blood flow and cutaneous vascular conductance do not support a redistribution of blood flow in the behavior trial (Figure 2 B&E). That said, it may be that changes in cutaneous vasomotor tone do not accurately reflect changes in visceral blood flow and/or volume. Nevertheless, our data support the idea that conventional measures of thermometry may not always reflect changes in heat exchange in dynamic cooling situations. For instance, common thermometry measurements (i.e., rectal temperature) likely underestimate heat storage when cool fluids are ingested because heat exchange from cool fluid and low blood flow in the viscera has a residual effect on the thermometry measurement (3, 7).

A further interesting finding of the present study relates to our skin wettedness responses. We have recently established that skin wettedness is a powerful contributing factor to thermal behavior (55). The present study, however, revealed no differences in skin wettedness between trials, despite that thermal discomfort was alleviated in the behavior trial. Notably, skin wettedness is the ratio of the difference between the absolute partial pressure of water on the skin and in the air, to the difference in total partial pressure of water on a saturated skin and in the air. Hence, the absolute skin humidity may be the more important driver of thermal behavior. This conjecture is supported by the fact that in the behavior trial, thermal comfort was maintained alongside attenuated skin humidity (Table 1). Although speculative, further studies should aim to investigate the role that absolute skin humidity plays in thermal discomfort and behavioral thermoregulation during exercise.

Collectively, behavioral thermoregulation was employed in the present study, eliciting voluntary reductions in skin temperature that elevated dry heat loss while proportionally lowering evaporative heat loss during light intensity exercise. Irrespective of the heat loss mechanisms, however, thermal discomfort was alleviated. While it is well established that sweat evaporation is a powerful heat loss mechanism, our data suggest that promoting convective heat loss through behavioral mechanisms that result in increased dry heat loss can also be effective in alleviating thermal discomfort without affecting core temperature during exercise.

Considerations

It is important to highlight some limitations of the present study. Firstly, it should be noted that the present findings are specific to the conditions employed herein (i.e., thermoneutral ambient temperatures, moderate humidity levels and light intensity exercise) and cannot likely be translated to warmer environments and/or higher exercise intensities. Likewise, in this study, we only allowed for manipulation of dry heat exchange. Therefore, we are unaware how thermal behavior (and the subsequent thermal and perceptual responses) may differ if the behavioral response improved evaporative heat loss. Further to this, we tested our females in the first 10 days of their menstrual cycle. However, we did not confirm the menstrual cycle phase via hormonal analyses. Although we are confident that our results are representative of females when estrogen and progesterone are at their lowest levels, we also recognize that thermal behavioral responses have been shown to be similar in females across the menstrual cycle, thus the importance of testing within the cycle phase may be reduced (28). Nevertheless, there are differences in autonomic temperature regulation and perceptual responses that have been documented in females and therefore, further research is warranted in this area (37, 39). To complicate this limitation further, a subset of our female participants were taking oral contraceptives. This is important to note as attenuated sudomotor responses have been documented in well-trained females on oral contraceptives (27). However, this limitation was likely minimized given our use of a crossover design where each subject served as their own control. While the present study was not designed to asses sex differences, we have previously seen differences in thermal behavior between males and females (58) and thus, it would have been ideal to determine if those differences were apparent in the present study as well. It is also possible that the core temperature pill used in this study was influenced by the visceral redistribution of blood flow. Our subjects ingested the telemetry pill only 60 min prior to exercise. A delimitation to this method is the reduced time for entry into the gastrointestinal tract and that we restrict subjects from eating or drinking after ingesting the pill. Nevertheless, esophageal temperature may have been a better index of core temperature due to its greater temporal resolution (32) and minimal influence of visceral redistribution of blood flow (49). Additionally, in the present study, engaging in thermal behavior only required subjects to press a button (i.e., it was easy). Thus, this model may not accurately test the external validity of engaging in thermal behavior in everyday life where we often have to work for, or find motivation to engage in thermal behavior (i.e., get off the couch to turn the air conditioner on). It would be important to identify if thermal behavior is still able to alleviate thermal discomfort in instances when subjects are presented with a motivational conflict (i.e., performing muscular work) to engage in thermal behavior. Finally, we performed partitional calorimetric calculations post hoc to further delineate the greater rise in core temperature in the behavior trial and to determine if there was greater heat storage. That said, the complexity of calculating heat loss and gain through the water perfused suit top required further partitioning of body surface area and correction factors (i.e., one for dry heat loss to and from the environment, and one for evaporative resistance of the suit and compression top) to be determined. It is possible that our correction factors may slightly over or under estimate actual heat exchange. Additionally, these correction factors do not consider a possible reduction in insulation of the water perfused top due to wetting of the suit or reduction in temperature of the water perfused top due to evaporation of sweat. Finally, another consideration is the use of a two compartment, rather than three compartment system for calculating partitional calorimetry. It could be argued that the surface area outside of any clothing, under clothing but not touching the tubes, and underclothing directly touching tubes, would provide a more accurate representation of the heat losses presented within this manuscript. However, estimating a third compartment would be difficult to do, post hoc, as we were not able to identify exactly how much of each area of the torso was in direct contact with the tubes. Nevertheless, these factors and assumptions were applied to all individuals, across all trials, and thus corrected for systematic errors. While there are some limitations to our calculations, we believe they represent accurate heat exchange to the best of our ability when considering it post hoc.

Perspectives

The present study indicates that thermal behavior resulting in large reductions in mean skin temperature is effective at alleviating thermal discomfort during exercise, and appears to involve a trade-off whereby dry heat loss is augmented, despite engaging in thermal behavior that attenuates evaporative heat loss. These findings may have broad impacts for athletes, workers, and clinical populations. Specifically, applying convective cooling is effective at promoting thermal comfort (or minimizing thermal discomfort) without meaningfully affecting core temperature. Thus, individuals who have an attenuated sweating response, such as the older adults (18) those with Multiple Sclerosis (1), or burn survivors (36), may directly benefit from voluntarily engaging in thermal behavior that promotes convective cooling. Notably however, behavioral thermoregulation during exercise has rarely been assessed in these populations. This is an important oversight given the potential barrier that ‘feeling too hot’ plays in regularly engaging in physical activity and/or adhering to an exercise regimen (14, 51).

Conclusions

During light intensity exercise, thermal behavior that results in reductions in mean skin temperature can alleviate thermal discomfort and promote heat loss. This improvement in thermal discomfort was elicited by voluntary reductions in skin temperature that augmented dry heat loss, but suppressed sweat production and evaporative heat loss. Importantly, engaging in thermal behavior did not meaningfully affect core temperature.

Acknowledgements

We would like to extend our thanks to all subjects who participated in the study. We would also like to thank lululemon athletica inc. for financially supporting the study. All authors contributed to this study. RG is the Research Director for the Whitespace Innovation Team at lululemon athletica inc. RG, ZS, NV and BJ contributed to the conceptualization of this study. NV and CC were responsible for all data collection and processing. NV performed data analyses and drafting of the manuscript. All authors approved the final manuscript. ZJ and NV have received travel reimbursement from lululemon athletica inc. There are no other conflicts of interest to report.

Appendix A. Metabolic Heat Production Calculations

Estimates of metabolic heat production (H_{prod}) were calculated via partitional calorimetry in watts (W), using the following equation:

(1) $$H_{prod} = M - Wk \text{ (W)}$$

where M is the metabolic energy expenditure, calculated in equation (2) below and Wk is the external workload calculated in equation (3) below (24):

(2) $$M = VO_2 \cdot \frac{\left[\left(\frac{RER-0.7}{0.3}\right) \cdot 21.13\right) + \left(\left(\frac{1.0-RER}{0.3}\right) \cdot 19.62\right)}{60} \cdot 1000 \quad \text{(W)}$$

where RER is the respiratory exchange ratio. And 21.13 represents the caloric equivalent per liter oxygen for the oxidation of carbohydrate, and 19.62 that for oxidation of fat (24).

(3) $$Wk = rpm \cdot kp \quad \text{(W)}$$

where rpm is the cadence and kp is the kilopond resistance applied to the ergometer.

Appendix B. Skin Wettedness Calculations

Local skin wettedness was calculated at each site as the ratio between the evaporative heat flux gradient between the humidity at the skin and in the air, and the maximal evaporative heat flux gradient for a totally wet skin (13, 17):

(4) $$W_{local} = \frac{P_{sk} - P_a}{P_{sk,s} - P_a} \quad \text{(a.u.)}$$

where P_{sk} is the measured water vapor pressure at the skin and P_a is the partial pressure of water in the atmosphere measured in kilopascals (kPa), calculated as:

(5) $$P_{sk} = \left(\frac{Rh_{sk}}{100}\right) \cdot P_{sk,s} \quad \text{(kPa)}$$

where Rh_{sk} is the relative humidity measured from the respective iButton, placed 6mm off the skin surface (56) and $P_{sk,s}$ is the saturated vapor pressure at the skin. P_a, can be calculated from equation (11) by substituting Rh_a as the relative humidity measured within the environmental chamber, and $P_{a,s}$ as the saturated water vapor pressure in the air. $P_{sk,s}$ can be calculated as:

(6) $$P_{sk,s} = 0.1 \exp\left(18.956 - \frac{4030.18}{T_{sk} + 235}\right) \quad \text{(kPa)}$$

and $P_{a,s}$ can be calculated using equation (6), substituting T_a for T_{sk} (2). Whole body skin wettedness was calculated as the unweighted average of all 8 sites.

Appendix C. Rate of Heat Storage Calculations

Due to the divergent conclusions that could be drawn based on the absolute and absolute change in in core temperature data between the behavior and control trials, post hoc analyses were performed to determine whether cumulative heat storage differed between trials. The rate of heat Storage (S) was calculated every 15 min during baseline and every 30 min during exercise. Heat storage was calculated as:

(7) $$S = H_{prod} - H_{dry} - H_{evap} - H_{res} \quad (W)$$

where H_{dry} represents the sum of dry heat losses from radiation and convection, H_{evap} represents heat loss from evaporation and H_{res} represents heat loss from respiration. The rate of heat loss from conduction was considered negligible and thus was eliminated from the equation (11). Calculations for H_{dry} and H_{evap} were performed for areas outside and under the suit and summed together to calculate total H_{dry} and H_{evap} losses. H_{dry} from convection and radiation outside the suit were calculated as:

(8) $$(C_{skin} + R_{skin})_{outside} = (T_{sk} - T_a) \times (h_r + h_c) \times BSA \quad (W)$$

where T_{sk} is the mean skin temperature of the legs and head, T_a is the ambient temperature of the environmental chamber, h_r and h_c are the estimated radiative and convective heat transfer coefficients, respectively and were calculated as previously described by Jay and Kenny (24). BSA was the body surface area not influenced by the water perfused suit top, estimated to be 60% (38). The ambient temperature was used as the air and radiant temperatures were assumed to be equivalent (11). H_{dry} from convection and radiation under the water perfused suit top was adapted from previous equations and calculated as:

(9) $$(C_{skin} + R_{skin})_{under} = \left(T_{bath_{out}} - T_{bath_{in}}\right) \times C_{p\_fluid} \times M_{fluid} \quad (W)$$

where T_{bath_out} was always 34ºC for the control trial, and calculated for each subject based on the number of behaviors performed during each 30 min block throughout the cycling protocol during the behavior trial. T_{bath_in} was directly measured as the temperature of the water immediately after perfusing the top. The C_{p_fluid} is the specific capacity of water, (4.184 $J \cdot g^{-1} \cdot {}^{o}C^{-1}$) and M_{fluid} is total mass of water perfusing the top in a 30 min period (6 L). A correction factor was applied to account for the dry heat lost (in the control trial) or gained (in the behavior trial) from the environment to the suit alone. To determine the correction factor, the suit was placed on a manikin equilibrated to an ambient temperature of 27ºC and 48% relative humidity to simulate average temperature and humidity in the experimental trials. The average T_{bath_out} temperature perfusing the suit for all subjects (Control: 34ºC; Behavior: 18.3ºC) was perfused through the suit top for 60 min. The temperature of the water immediately after perfusing through the top (T_{bath_in}) was also measured. The correction factor was calculated individually for the control and behavior trials as:

$$\text{(10)} \qquad H_{dry}\ \text{Correction Factor} = \left(T_{bath_{out}} - T_{bath_{in}}\right) \times C_{P_{fluid}} \times M_{fluid}\ (W)$$

for each 30 min period and averaged together. These factors were 56.8 W of heat lost from the suit to the environment when 34ºC water perfused the suit top, and 58.2 W of heat gained to the suit from the environment when 18.3ºC water perfused through the top. The final corrected H_{dry} under the suit was calculated as:

$$\text{(11)} \qquad (C_{skin} + R_{skin})_{suit} = [(C_{skin} + R_{skin})_{uncorrected} - (C_{skin} + R_{skin})_{corrected}] \times BSA\ (W)$$

where BSA is the area directly in contact with the water perfused suit top, estimated to be 40% (38). All data were calculated in W and then converted to kJ. Dry heat loss from outside the suit and under the suit were summed together as a measure of total dry heat loss.

Heat loss from evaporation was also individually calculated for areas outside and under clothing. H_{evap} from outside the suit was calculated as:

$$\text{(12)} \qquad E_{outside} = h_e \times (P_{sk} - P_a) \cdot BSA\ \ (W)$$

where h_e is the product of the convective heat transfer coefficient and the Lewis Relation coefficient (16.5 K·kPa^{-1}), and accounting for the barometric pressure ($P_{b,}$ (mmHg)) and calculated as:

$$(13) \qquad h_e = 16.5 \times h_c \times \left(\frac{760}{P_b}\right) \ (\mathrm{W \cdot m^{-2} \cdot kPa^{-1}})$$

P_{sk} is the absolute partial pressure of water on the skin calculated from the relative humidity measured at the skin via each local iButton (equation 5 above), P_a is the absolute partial pressure of water in the air calculated from relative humidity and temperature (equation 5 above, substituting ambient relative humidity and temperature), and BSA is the relative body surface area inside or outside the water perfused top. P_{sk} was calculated using iButtons locally placed at the, calf, anterior thigh and forehead.

To determine evaporation from under the water perfused suit top, iButtons locally placed at the suprascapular area, shoulder, forearm, chest and abdomen were used. A correction factor was calculated to account for the evaporative resistance of the suit and compression top. To determine this correction factor, two post-hoc experiments were conducted. In both experiments, a water perfused mat (Gaymar T-Pad, Braintree Scientific Inc, MA, USA) was set to the average mean skin temperature under the top for the control (34.8ºC) or behavior (32.1ºC) trials. Four iButtons were set up to measure the absolute relative humidity at 1) distance of 6mm above the mat under the suit and compression top, 2) a distance of 2 mm above the suit and compression top, 3) a distance of 6 mm above the mat outside of the suit and compression top and 4) a distance of ~10 mm above the mat (the same height as iButton 2, but without impedance from the suit and compression top). For the respective control or behavior trial, the suit top and a single layer of the compression top were placed over the iButtons. The suit top perfused 34ºC for the control trial, and 18.3ºC for the behavior trial. A fully saturated paper towel was placed on top of the water perfused mat, underneath the iButton set up and the evaporation was measured for a 60 min period, as we have done previously (56). The partial pressure of water at the mat (P_{mat}) and at the garment ($P_{garment}$) were calculated from equations 16 below, averaging the first 20 min when the saturated paper towel mimicked the generation of sweat and a saturated skin. The correction factors (which were determined to be - Control: -0.58 kPa; Behavior: -0.95 kPa) were calculated as:

(14) $$P_{correction} = P_{mat} - P_{garment}$$

H_{evap} under the suit was calculated as:

(15) $$E_{under} = h_e \times (P_{sk} - (P_a - P_{correction)})) \times BSA$$

Finally, respiratory heat losses were calculated for evaporation (E_{res}) and convection (C_{res}) as:

(16) $$E_{res} + C_{res} = \left(0.0014 \cdot \left(H_{prod}\right) \cdot (34 - T_a)\right) + \left(0.0173 \cdot \left(H_{prod}\right) \cdot (5.87 - P_a)\right) \quad (W)$$

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Table 1 Physiological and perceptual skin wettedness responses to thermal behavior (n=12, mean ± SD). Skin wettedness, absolute water vapor pressure at the skin, perceptions of upper body skin wettedness and perceptions of whole body skin wettedness during light intensity exercise. #Different from 20 min baseline ($P<0.01$), *Behavior different from control ($P\leq0.03$).

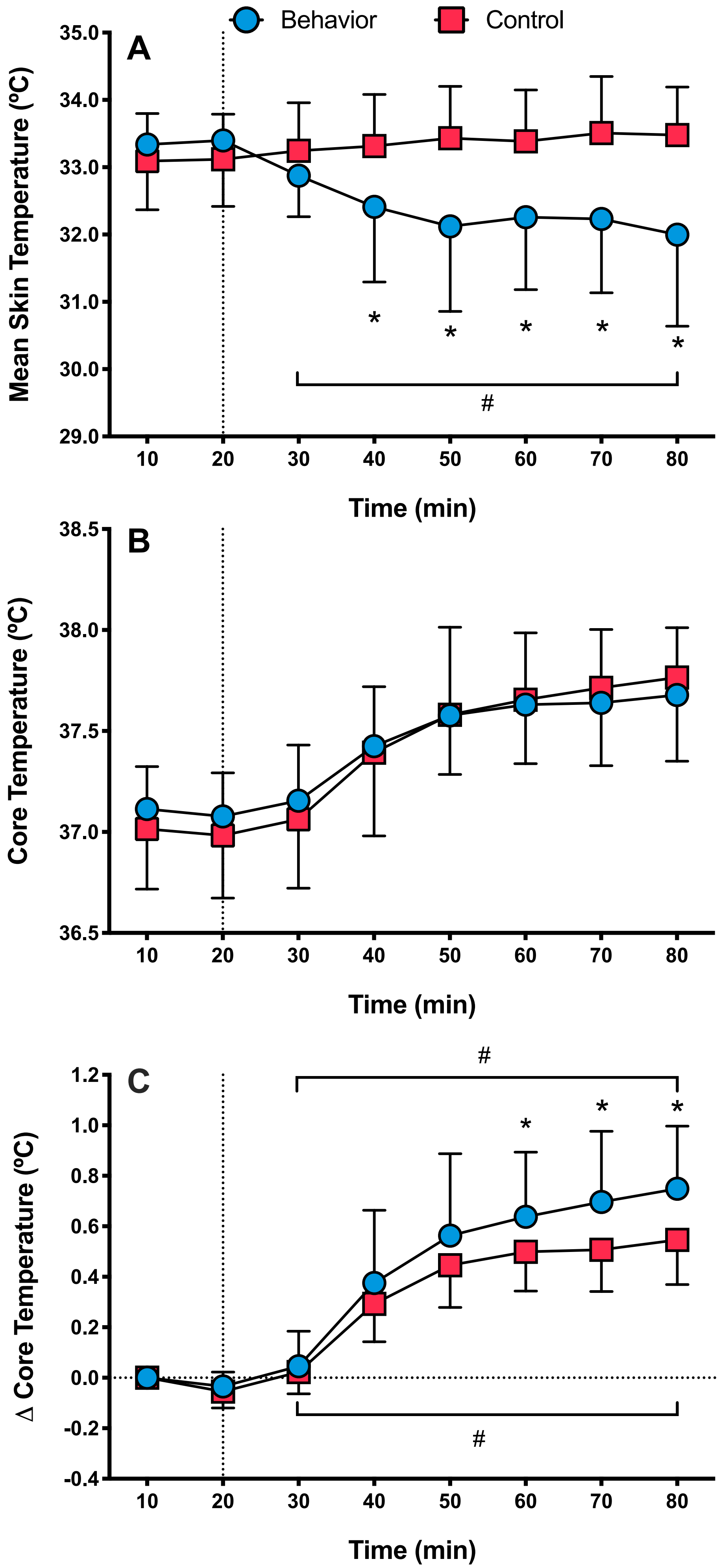
Figure 1 Body temperatures (n=12, mean ± SD). Mean skin temperature (A) and the change in (Δ) core temperature (B) during 60 min light intensity exercise (area after the vertical dashed line). #Different from 20 min baseline ($P<0.01$), *Behavior different from control ($P<0.01$).

Figure 2 Thermoeffector responses (n=12, mean ± SD). Water perfused top temperature (A), forearm skin blood flow (B), local axilla sweat rate (C) upper body skin temperature (D), forearm cutaneous vascular conductance (CVC) (E) and local thigh sweat rate (F) during 60 min light intensity exercise (area following the vertical dashed line). #Different from 20 min baseline ($P<0.04$), *Behavior different from control ($P\leq0.05$).

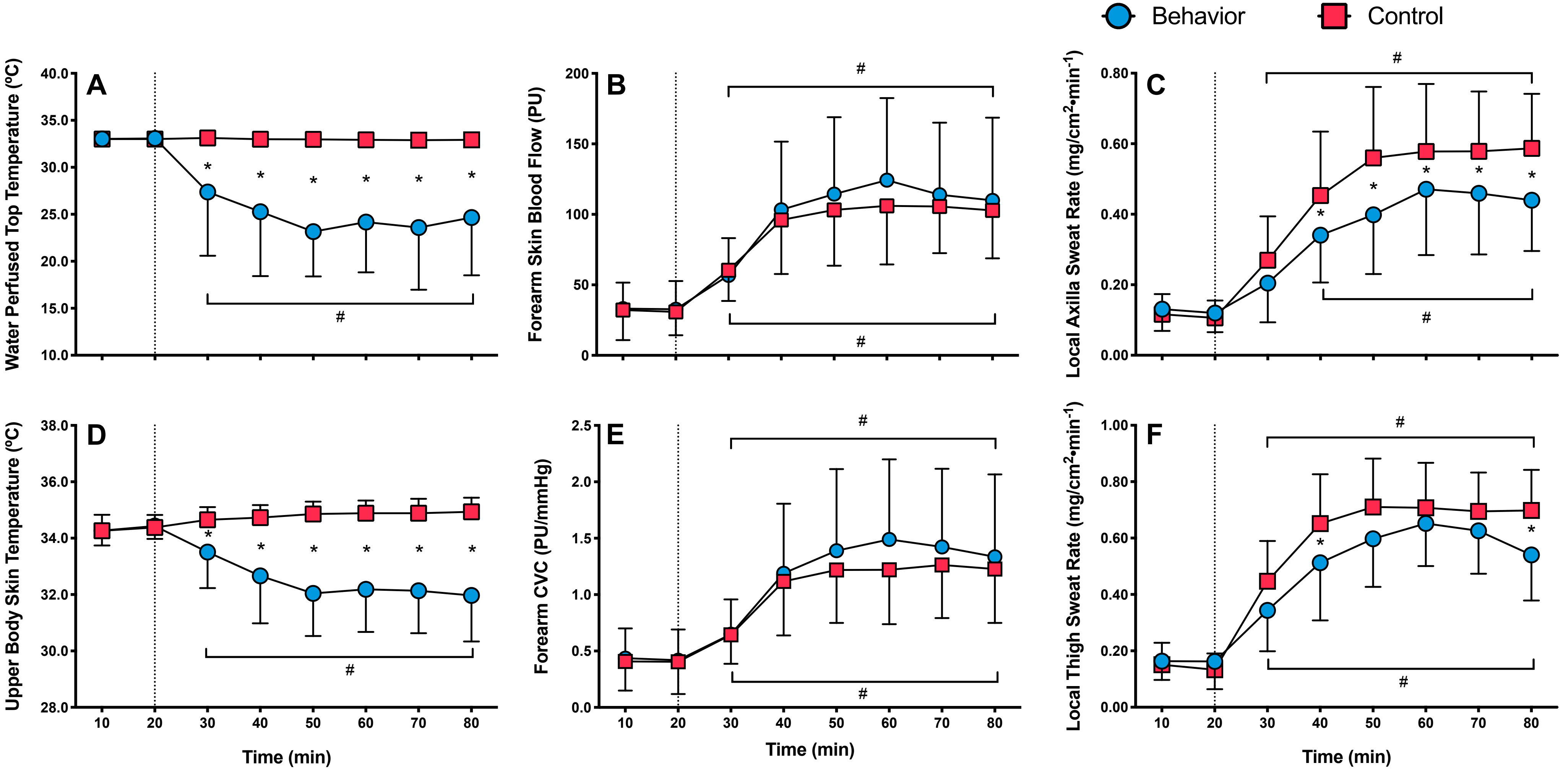
Figure 3 Upper body thermal sensation (A), whole body thermal sensation (B), upper body thermal comfort (C), whole body thermal comfort (D), upper body sweating (E), whole body sweating (F), upper body skin wettedness (G) and whole body skin wettedness (H) during exercise and recovery (n=12, mean ± SD). #Different from 20 min baseline ($P<0.01$), *Behavior different from control ($P\leq0.03$).

Figure 4 Estimated body heat losses (n=11, mean ± SD). Evaporative heat loss from outside the suit (A), evaporative heat loss from under the suit (B), total evaporative heat loss (C), dry heat loss from outside the suit (D), dry heat loss from under the suit (E) and total dry heat loss (F). #Different from 20 min baseline ($P<0.01$), *Behavior different from control ($P<0.01$).

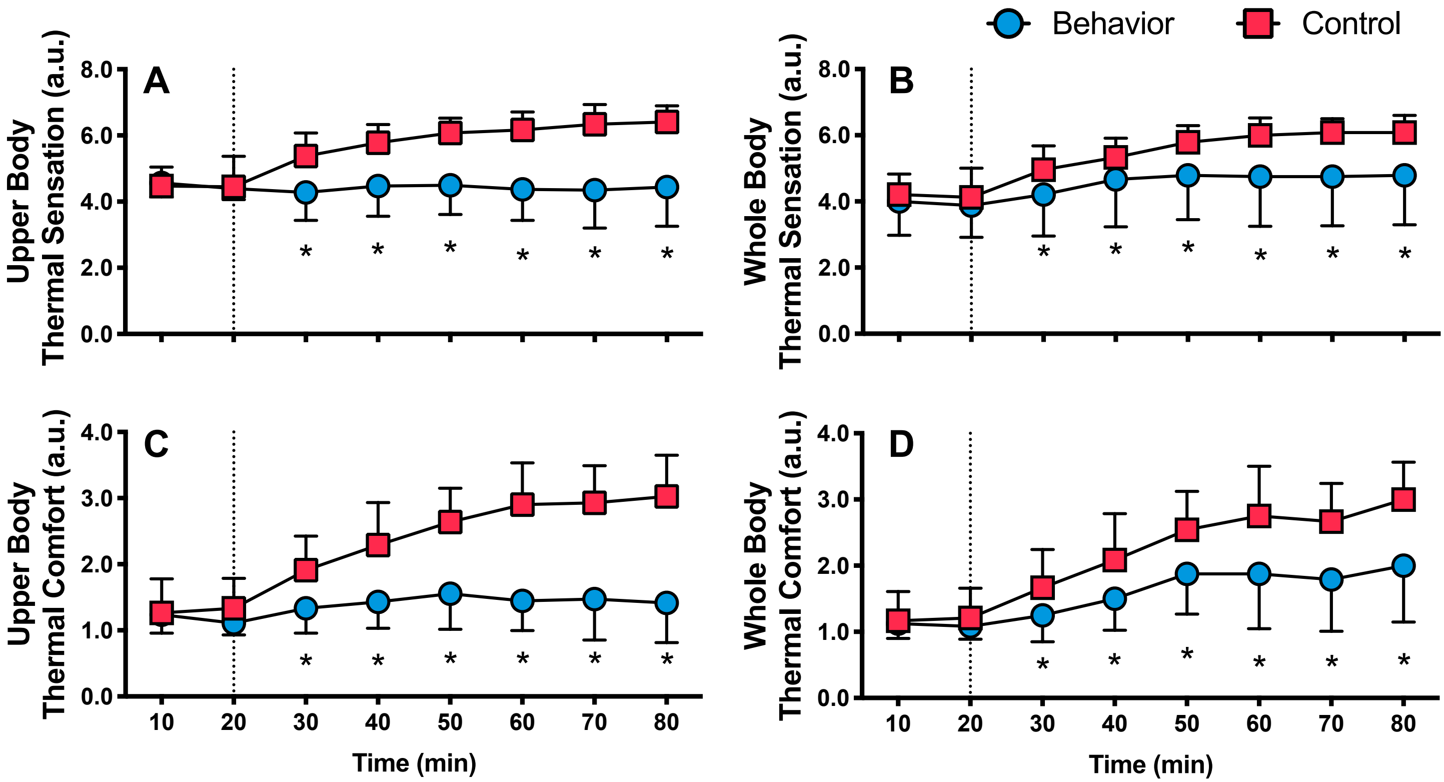
Figure 5 Body Heat Storage (n=11, mean ± SD) (A) and cumulative heat storage (B) after 60 min of light intensity exercise. [#]Different from 20 min baseline ($P<0.01$).

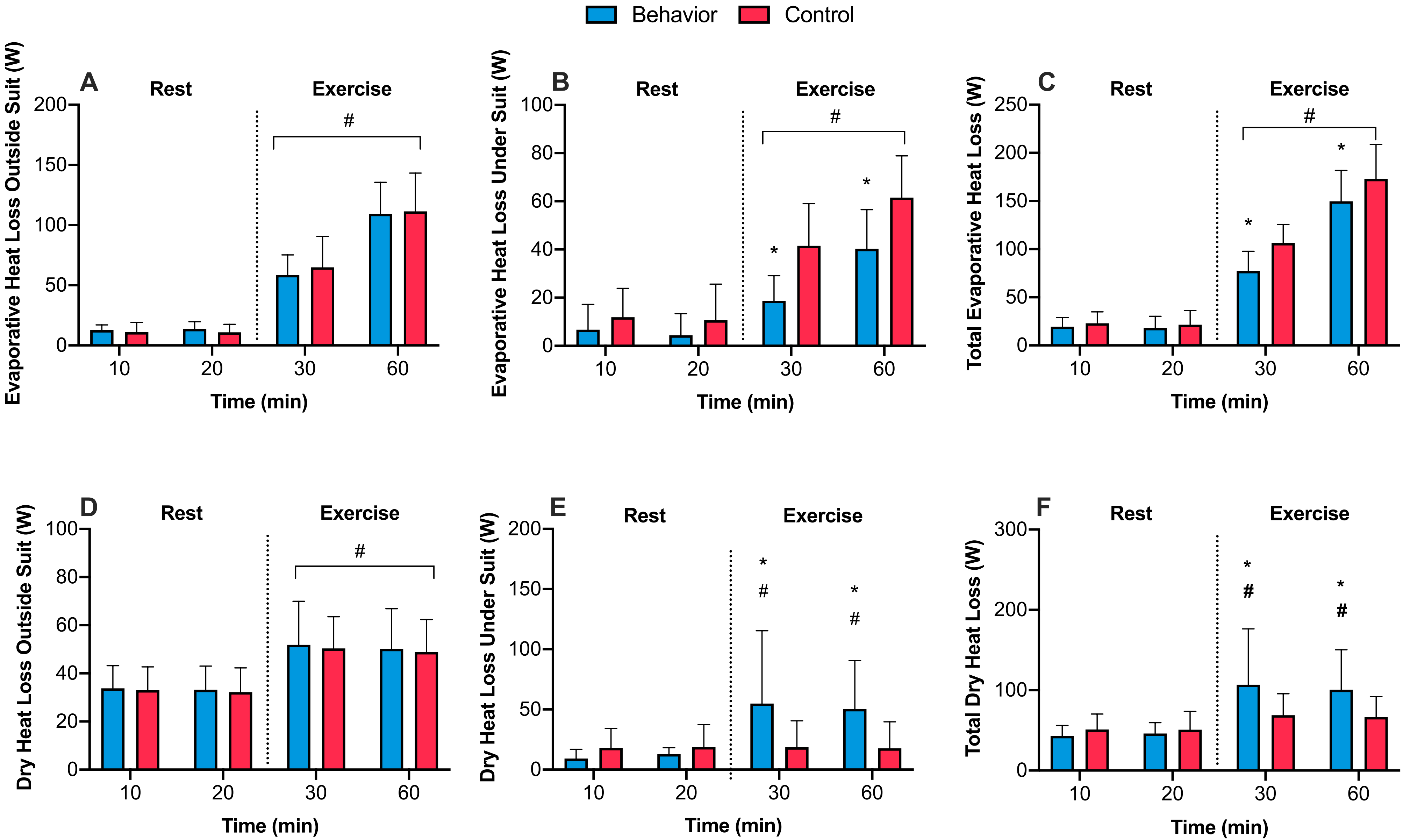


Behavior
Control
A
Mean Skin Temperature (ºC)
35.0
34.0
33.0
32.0
31.0
30.0
29.0
*
*
*
*
*
#
10
20
30
40
50
60
70
80
Time (min)
B
Core Temperature (ºC)
38.5
38.0
37.5
37.0
36.5
10
20
30
40
50
60
70
80
Time (min)
C
Δ Core Temperature (ºC)
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
#
*
*
*
#
10
20
30
40
50
60
70
80
Time (min)

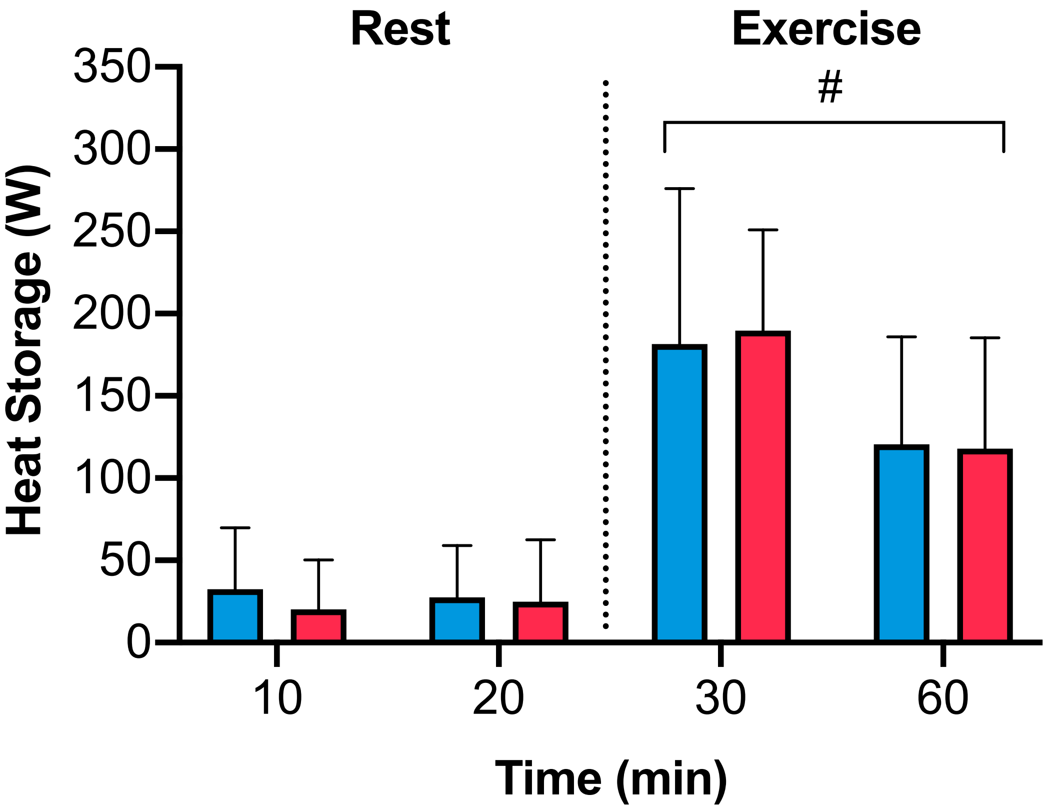


Behavior
Control
A
B
C
D
E
F
Water Perfused Top Temperature (ºC)
Forearm Skin Blood Flow (PU)
Local Axilla Sweat Rate (mg/cm2•min-1)
Upper Body Skin Temperature (ºC)
Forearm CVC (PU/mmHg)
Local Thigh Sweat Rate (mg/cm2•min-1)
Time (min)
Time (min)
Time (min)

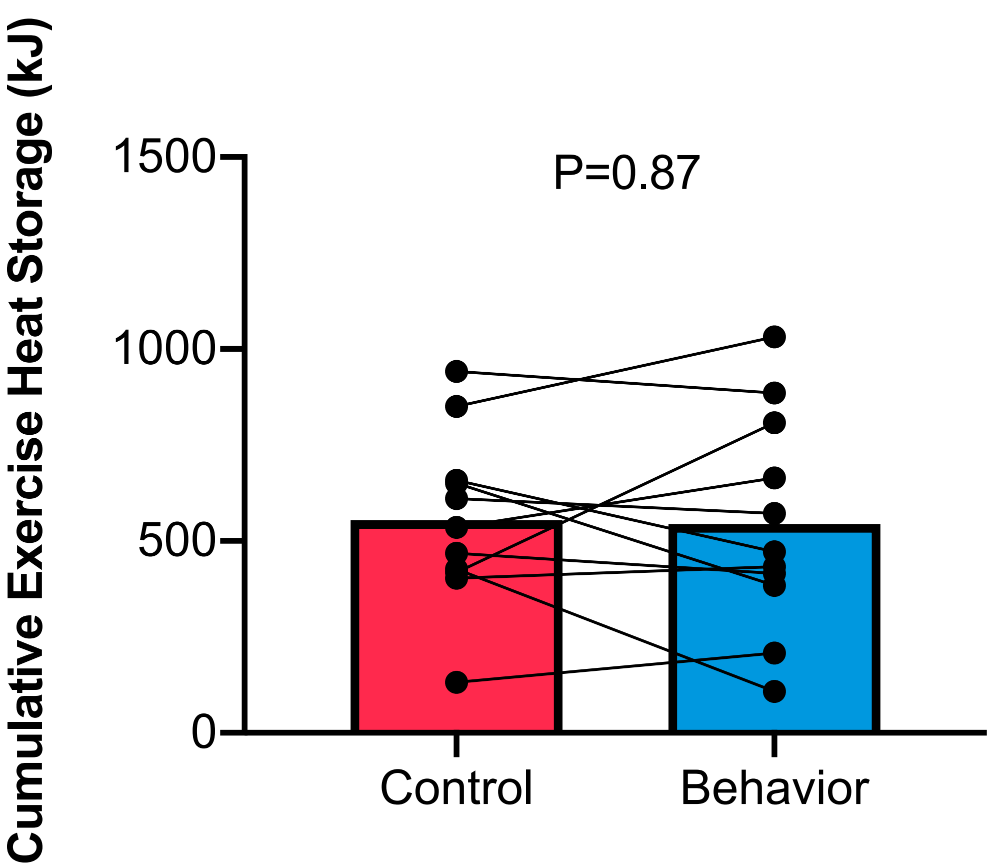

Behavior
Control
A
B
C
D
Upper Body Thermal Sensation (a.u.)
Whole Body Thermal Sensation (a.u.)
Upper Body Thermal Comfort (a.u.)
Whole Body Thermal Comfort (a.u.)
8.0
6.0
4.0
2.0
0.0
3.0
1.0
10
20
30
40
50
60
70
80
Time (min)
*



Behavior
Control
A
Rest
Exercise
#
Evaporative Heat Loss Outside Suit (W)
0
50
100
150
200
10
20
30
60
Time (min)
B
Rest
Exercise
#
*
*
Evaporative Heat Loss Under Suit (W)
0
20
40
60
80
100
10
20
30
60
Time (min)
C
Rest
Exercise
#
*
*
Total Evaporative Heat Loss (W)
0
50
100
150
200
250
10
20
30
60
Time (min)
D
Rest
Exercise
#
Dry Heat Loss Outside Suit (W)
0
20
40
60
80
100
10
20
30
60
Time (min)
E
Rest
Exercise
*
#
*
#
Dry Heat Loss Under Suit (W)
0
50
100
150
200
10
20
30
60
Time (min)
F
Rest
Exercise
*
#
*
#
Total Dry Heat Loss (W)
0
100
200
300
10
20
30
60
Time (min)



Rest
Exercise
#
Heat Storage (W)
350
300
250
200
150
100
50
0
10
20
30
60
Time (min)



Cumulative Exercise Heat Storage (kJ)
P=0.87
1500
1000
500
0
Control
Behavior

		Pre	Exercise (min)					
	Condition	20 min baseline	10	20	30	40	50	60
Physiological Variable								
Skin Wettedness (a.u.)	Control	0.20 ± 0.11	0.17 ± 0.09	0.50 ± 0.13#	0.68 ± 0.06#	0.69 ± 0.07#	0.69± 0.07#	0.69 ± 0.06#
	Behavior	0.19 ± 0.09	0.14 ± 0.06	0.44 ± 0.15#	0.66 ± 0.03#	0.68 ± 0.05#	0.71 ± 0.03#	0.70 ± 0.03#
Absolute water vapor pressure at the skin (kPa)	Control	2.49 ± 0.53	2.39 ± 0.50	3.57 ± 0.52#	4.09 ± 0.32#	4.18 ± 0.32#	4.23 ± 0.34#	4.24 ± 0.31#
	Behavior	2.45 ± 0.54	2.26 ± 0.46	3.10 ± 0.59#*	3.73 ± 0.43#*	3.87 ± 0.41#*	3.93 ± 0.41#*	3.87 ± 0.41#*
Perceptual Variable								
Upper body skin wettedness (a.u.)	Control	-0.2 ± 1.2	0.9 ± 0.7#	1.7 ± 0.6#	2.0 ± 0.5#	2.4 ± 0.4#	2.5 ± 0.3#	2.5 ± 0.3#
	Behavior	0.0 ± 0.7	0.2 ± 0.8	1.0 ± 0.3#*	1.3 ± 0.4#*	1.4 ± 0.7#*	1.6 ± 0.5#*	1.7 ± 0.6#*
Whole body skin wettedness (a.u.)	Control	-0.5 ± 1.0	0.8 ± 0.7#	1.4 ± 0.5#	1.9 ± 0.5#	2.2 ± 0.4#	2.1 ± 0.4#	2.2 ± 0.3#
	Behavior	0.0 ± 01	0.4 ± 0.4	1.2 ± 0.8#	1.5 ± 1.0#	1.9 ± 1.1#	2.0 ± 1.0#	2.1 ± 1.2#